INTRODUCTION

onnative grass invasions can increase fire intensity by increasing the loading, continuity, and flammability of fine fuels (Balch and others 2013, Fuentes-Ramirez and others 2016, Fusco and others 2019, Setterfield and others 2010). Increased fire intensity, in turn, can shift ecosystem dynamics by promoting nonnative, invasive grasses over native plants, creating a positive feedback between fire and invasion (D'Antonio and Vitousek 1992). Although this grass-fire feedback has been documented in temperate deciduous forests (Flory and others 2015, Kerns and others 2020, Wagner and Fraterrigo 2015), the consequences for regeneration dynamics remain uncertain.

In temperate deciduous forests, fire favors the establishment of species with fire-adapted traits, such as hypogeal germination, resprouting ability, and thick bark (Arthur and others 2012; Brose and Van Lear 1998, 2004). However, the responses of fire-adapted and other temperate deciduous species to increases in fire intensity are poorly understood. On the one hand, seedlings may tolerate increased fire intensity because they have well-developed root systems and stores of carbohydrates that promote resprouting (Bond and Midgley 2001, Bowen and Pate 1993). On the other hand, invasive grasses can outcompete native woody vegetation for resources owing to their dense roots, high nutrient efficiencies, and rapid growth rates (Grice and others 2013, Marshall and others 2009). Strong resource competition could reduce tree carbohydrate reserves, especially in small individuals, thereby limiting resprouting

ability (Villar-Salvador and others 2015). Additionally, small individuals are more prone to fire-induced injuries (Brando and others 2012) and may therefore experience higher mortality rates. With fire increasingly used to maintain and restore temperate forests (Stephens 2005) and with widespread grass invasions in forests (Iannone and others 2016), there is a critical need to determine how invasion affects post-fire tree persistence to guide management and anticipate future forest dynamics.

We examined how invasion by the shadetolerant, C4 grass Microstegium vimineum (Nepalese browntop, or stiltgrass) interacts with prescribed fire to affect the regeneration of naturally established seedlings and saplings of varying sizes. M. vimineum is widespread in temperate forests in the Eastern United States, currently spanning 26 States (USDA NRCS 2020). Previous studies show that once established, M. vimineum can strongly compete with native understory plants for resources (Ehrenfeld and others 2001, Flory and Clay 2009, Marshall and others 2009), although this effect diminishes with canopy closure (Daniels and Larson 2020, Flory and others 2017). M. vimineum has also been found to increase fire intensity and the mortality of planted tree seedlings (Flory and others 2015), yet the interactive effects of fire and invasion on naturally established juvenile trees are less clear. We expected that naturally established juvenile trees would be resilient to grass-fire interactions because of their ability to resprout. However, because size influences resprouting ability and vigor (Gilbert and others 2003, Matula and others 2019) as well as vulnerability to heating-induced

CHAPTER 8

Evaluating the Effects of Nonnative Grass Invasion on Fuels, Fire Behavior, and Tree Regeneration in the Central Hardwoods Region

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mortality, we expected smaller trees would be less resilient than larger trees, potentially leading to long-term shifts in regeneration dynamics. We tested these predictions in the context of the following three objectives: (1) quantify differences in fire intensity and its drivers between invaded and uninvaded plots; (2) determine how fire intensity and *M. vimineum* invasion affect the regeneration of tree seedlings and saplings with respect to size; and (3) evaluate the potential long-term effects of prescribed fire and *M. vimineum* invasion on stand development using a forest growth and yield simulation model.

METHODS

As described in Salemme and Fraterrigo (2021), in August 2015 we established twenty 0.04-ha pairs of invaded and uninvaded (control) plots (n =40 plots total) spanning the range in soil moisture conditions present and distributed across six Forest Service, U.S. Department of Agriculture, management units at Shawnee National Forest in southern Illinois. Stands were dominated by oak (Quercus spp.) and hickory (Carya spp.) in drier areas and shortleaf pine (Pinus echinata) and tuliptree (Liriodendron tulipifera) in wetter areas. Prescribed fire had previously been applied in each of the management units one to three times. Invaded plots had at least 70-percent M. vimineum surface cover. In the fall prior to prescribed fire application, we determined surface litter, M. vimineum biomass, and coarse woody fuel biomasses in each plot. Woody fuel samples were collected immediately prior to burning to determine fuel moisture content. Volumetric

soil moisture was measured monthly throughout the growing season. Additionally, tree seedlings (≤1 m in height) in each plot were identified to species, tagged, and measured for stem height and diameter at ground level (seedlings) or breast height (saplings). Overall, we tagged 419 seedlings and 157 saplings.

Between October 2015 and February 2017, prescribed fire was applied to all management units. To quantify fire behavior, we recorded fire temperature and residence time using a K-type thermocouple coupled with a data logger and determined flame length by measuring the maximum height of scorch marks. Weather conditions preceding fires and on fire days were determined from nearby weather stations. Fuels were resampled following fire to determine consumption. To determine post-fire seedling and sapling persistence, defined here as trees that survived or resprouted post-fire, we relocated tagged trees in July of the following growing season and recorded their survival status (survived, resprouted, or other). Seedlings that did not survive or resprout in the growing season following fire were reassessed after an additional growing season; if they still showed no signs of growth, they were considered dead.

We simulated post-fire tree regeneration decadally from 2016–2066 using the Central States variant of the Forest Service Forest Vegetation Simulator (FVS) and the Fire and Fuels Extension (FFE) to the FVS (Rebain 2010). Simulated stands were initialized using field data for each plot. To examine the effects of grass invasion and prescribed fire on tree

regeneration, we modeled four different scenarios: low-intensity, uninvaded; low-intensity, invaded; moderate-intensity, uninvaded; and moderate-intensity, invaded. For each scenario, we adjusted the following parameters: flame height, percentage of stand area burned, and the number of sprouts multiplier using field data from our study and from a similar study involving *M. vimineum* and prescribed fire in a midwestern temperate forest (Flory and others 2015).

To evaluate the relationships between grass invasion, fuel conditions, and fire behavior, we used linear mixed effects models. To test for differences in post-fire seedling and sapling persistence and resprouting probabilities, we used generalized linear mixed models. In both cases, we included burn unit as a random effect. We used structural equation modeling to quantify the relative magnitude of direct and indirect effects of M. vimineum invasion and fire intensity on seedling survival. Finally, to evaluate the effects of invasion status and prescribed burning on FVS-simulated tree resprouting, we compared the average number of resprouts per time step (decadal) by invasion status for each fire intensity scenario described above using paired t-tests. All analyses were performed in R.

RESULTS

Total fuel loading and woody fuel moisture did not differ with invasion status; however, nonwoody surface litter moisture was nearly 50 percent higher in invaded than uninvaded plots (Salemme and Fraterrigo 2021). *M. vimineum* biomass accounted for roughly 10 percent of

nonwoody litter biomass in invaded plots and was significantly higher in areas of high soil moisture. As a result of these moisture differences, fires in invaded plots had 33-percent-lower flame length, 45-percent-lower percentage of area burned, and 40-percent-shorter fire residence time than uninvaded plots (fig. 8.1). Fire-weather and site conditions, mainly air temperature and soil moisture, were the strongest predictors of fire behavior (Salemme and Fraterrigo 2021).

Prior to fire, invaded plots had significantly lower seedling densities than uninvaded plots, with 43.5 percent fewer seedlings on average. Invaded plots also had significantly fewer small-sized individuals than uninvaded plots (table 8.1). Pre-fire sapling density did not vary between invaded and uninvaded plots.

Fire reduced seedling persistence by 40 percent compared to unburned plots. There was no statistical interaction between fire and invasion. Among burned plots, however, invaded plots had 54-percent-lower seedling persistence than uninvaded plots, despite experiencing lower fire intensity and having larger individuals (fig. 8.2). On average, the diameter of seedlings with a 50-percent probability of persistence was 2.8 times higher in invaded than uninvaded plots, suggesting invasion reduced the resilience of smaller individuals to fire. Supporting this, resprouting probability was positively related to diameter, while invasion had a marginal negative effect. The structural equation model indicated a direct negative effect of M. vimineum biomass and an indirect negative effect of fire intensity on seedling persistence, with the effect size of

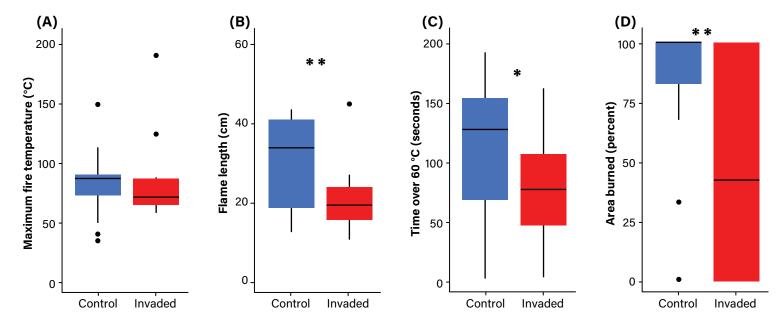


Figure 8.1—Boxplots of (A) maximum fire temperature, (B) flame length, (C) residence time over 60 °C, and (D) percentage of area burned in uninvaded (control) and Microstegium vimineum-invaded plots. Data are averaged across 2015–2017 prescribed fires. Asterisks indicate statistical significance (** = p < 0.05; * = p < 0.10).

Table 8.1—Pre-fire diameter-class distribution for tagged seedlings in control and invaded plots

	Seedling diameter class						
	0–2 cm	>2-4 cm	>4-6 cm	>6-8 cm	>8–10 cm	>10-12 cm	>12 cm
Control	52	98	65	36	17	5	0
Invaded	13	43	51	23	12	3	1

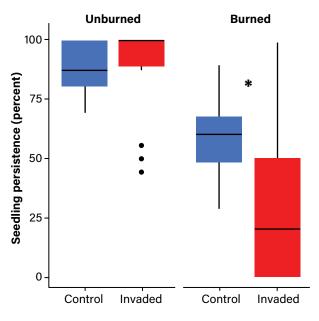


Figure 8.2—Boxplots of seedling persistence by invasion and fire status. Data are averaged across 2015–2017 prescribed fires. While there was no interactive effect of fire and invasion, persistence in burned-invaded plots was lower than in burned-uninvaded plots. Asterisk indicates statistical significance (* = p < 0.01).

M. vimineum more than twice that of fire. There was also a direct positive effect of seedling diameter on persistence. Although fire reduced sapling persistence by 28 percent compared to unburned plots, there were no significant differences in sapling survival by invasion or diameter among burned plots.

The partial establishment model in the FVS Central States variant simulates resprouting from stumps or roots based on stand density, parent tree size, and species resprouting potential (FVS Staff 2008). We parameterized the number of sprouts multiplier within FVS to further reflect observed differences in post-fire tree regeneration. Averaged over a 10-year time step, we found that FVS-simulated resprouting differed with invasion under both low- and moderate-intensity fires. Invasion resulted in a 63-percent reduction in resprout density compared to uninvaded plots.

DISCUSSION AND CONCLUSIONS

Previous studies show that invasive grass-fire feedbacks can increase fire intensity in temperate deciduous forests (Wagner and Fraterrigo 2015), resulting in decreased survival of recently planted but not naturally established juvenile trees (Flory and others 2015). In contrast, we found that grass invasion reduced the intensity of prescribed fire. Despite having lower fire intensity, post-fire persistence and resprouting of naturally established seedlings was lower in invaded than uninvaded plots, whereas persistence was unaffected by invasion in the absence of fire (Salemme and Fraterrigo 2021). Structural equation modeling also demonstrated that

the magnitude of the direct negative effect of invasion on post-fire seedling persistence was greater than the negative indirect effect via fire intensity. Collectively, these results suggest that grass invasion can reduce forest resilience to fire by inhibiting the regeneration and growth of seedlings. Consequently, temperate deciduous forests that have historically been maintained or restored by periodic fire may no longer experience the same benefits from burning when invaded by nonnative grasses.

Our results reveal that soil moisture was a strong driver of fire intensity and that the moisture content of nonwoody surface fuels was considerably higher in invaded than uninvaded plots. These patterns coincided with 11-percentgreater precipitation during the spring 2016 burn season than the 15-year average (WARM/ICN 2019). A previous study conducted at comparable sites in Shawnee National Forest demonstrated that burning under drier conditions resulted in higher fire residence times in M. vimineuminvaded plots (Wagner and Fraterrigo 2015). Collectively, these findings underscore the overarching effect of climate and meteorological events on fire intensity regardless of invasion status and suggest we may have observed more intense fires and possibly lower tree survival if fires were conducted under drier conditions.

Despite lower intensity fires, fewer seedlings persisted following fire in invaded plots, with stem diameter moderating this effect. The observed post-fire persistence rate in invaded plots averaged 31 ± 7 percent. Similarly, grass invasion reduced post-fire survival of planted

seedlings by 54 percent in southeastern Indiana (Flory and others 2015) and significantly reduced species richness of naturally recruited woody species in a northern Mississippi oakhickory woodland (Brewer and others 2015). The difference in seedling survival rate by invasion, together with the difference in resprouting rate, suggests that M. vimineum invasion has both direct and indirect effects on post-fire seedling persistence, a hypothesis supported by the results of the standard error of the mean. The marginal difference in resprouting could be caused by prolonged nitrogen immobilization, associated with both grass invasion (Ehrenfeld and others 2001) and repeated burning (Fraterrigo and Rembelski 2021, Hernández and Hobbie 2008), which has been shown to reduce the storage of nonstructural carbohydrates in woody plants and decrease seedling resprouting capabilities (Villar-Salvador and others 2015). Additionally, grass invasion may have resulted in fire burning closer to the root collar of seedlings by increasing within-plot fuel continuity, as even the low flame temperatures observed in invaded areas were high enough to damage root collars (Levitt 1980). In line with other studies (Flory and Clay 2010, Oswalt and Oswalt 2010, Oswalt and others 2007), we observed significantly lower pre-fire seedling densities and reduced numbers of small trees in invaded plots. All the management units in our study had previously been burned, so this pattern may be the result of past filtering of small individuals by grass-fire interactions.

Our results have important implications for managing grass-invaded temperate forests with fire. This study and others show that invasion can have varying effects on fire intensity depending on weather conditions, with dry conditions resulting in increased fire intensity and high mortality rates for planted seedlings (Flory and others 2015) and wet conditions having the opposite effect (Pilliod and others 2017, Poulos and Roy 2015). We further demonstrate that grass invasion can negatively affect tree regeneration by inhibiting the recovery of small seedlings from fire, likely through a combination of increasing resource competition and fine-scale increases in fire intensity. Further, our FVS simulations suggest that the interactive effects of fire and invasion on seedling resprouting alter longterm tree regeneration dynamics. Therefore, if a management goal is to promote the regeneration of shade-intolerant tree species, the time between fire applications may need to be lengthened to allow juvenile trees in invaded areas to reach a "safe" size (i.e., 7-10-mm stem diameter), at which the likelihood of persistence is higher.

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